DISCOHELIX (ARCHAEOGASTROPODA, EUOMPHALACEA) AS AN INDEX FOSSIL IN THE TETHYAN JURASSIC

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ABSTRACT. Morphological features, growth, mode of life, and stratigraphical distribution are examined in more than 300 extremely well-preserved specimens of *Discohelix* from the Sicilian Lower and Middle Jurassic. In some species parabolic ribs similar to those in ammonites are formed owing to resorbtion during brief discontinuities in growth. Deviated peristomes recurring at an angle of more or less 72° and resulting in a pentagonal outline of the shell, are developed in two species for which the new subgenus *Pentagonodiscus* (type species *D.* (*P.*) *angusta* n. sp.) is established. Ten species of *Discohelix* sensu stricto are described, five of which are new: *D. dictyota*, *D. conica*, *D. centricosta*, *D. costata*, and *D. levis*. The short stratigraphical ranges of the representatives of the genus are proved here for the first time and may be useful for the division of cephalopod-free series in the Tethyan Jurassic.

FEW genera of the widely distributed Palaeozoic Euomphalacea crossed the Permo-Triassic boundary and the superfamily became extinct in the Upper Cretaceous. In contrast to its Palaeozoic representatives, amongst which Knight (1934, p. 145) was even able to recognize some with value as index forms, those in the Mesozoic have neither been investigated in quantity nor in relation to their stratigraphical occurrence. Both these omissions can now be corrected using an individually and specifically rich gastropod fauna from the Jurassic of Sicily, of which members of the genus *Discohelix* are the chief element. The accompanying ammonites have usually allowed all the specimens to be zonally dated, so far as strong condensation permits such accuracy. A total of more than 300 *Discohelix*, extremely well preserved and with complete shells, have been collected from several Jurassic sections in western Sicily (Rocca Busambra). The only drawback is the recrystallization of the shell material which has left its structure difficult to recognize. Several specimens from the Liassic of the Northern Calcareous Alps, the originals of Stoliczka (1861) from the north alpine Hierlatz facies, and those of Quenstedt (1884) and Brösamlen (1909) from the south German epicontinental Jurassic have been available for comparison.

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MORPHOLOGY

Protoconch

Because of the more or less planispiral coiling of the shell, the larval whorls are almost always preserved, so that the sculpture of the earliest ontogenetic stages can be precisely

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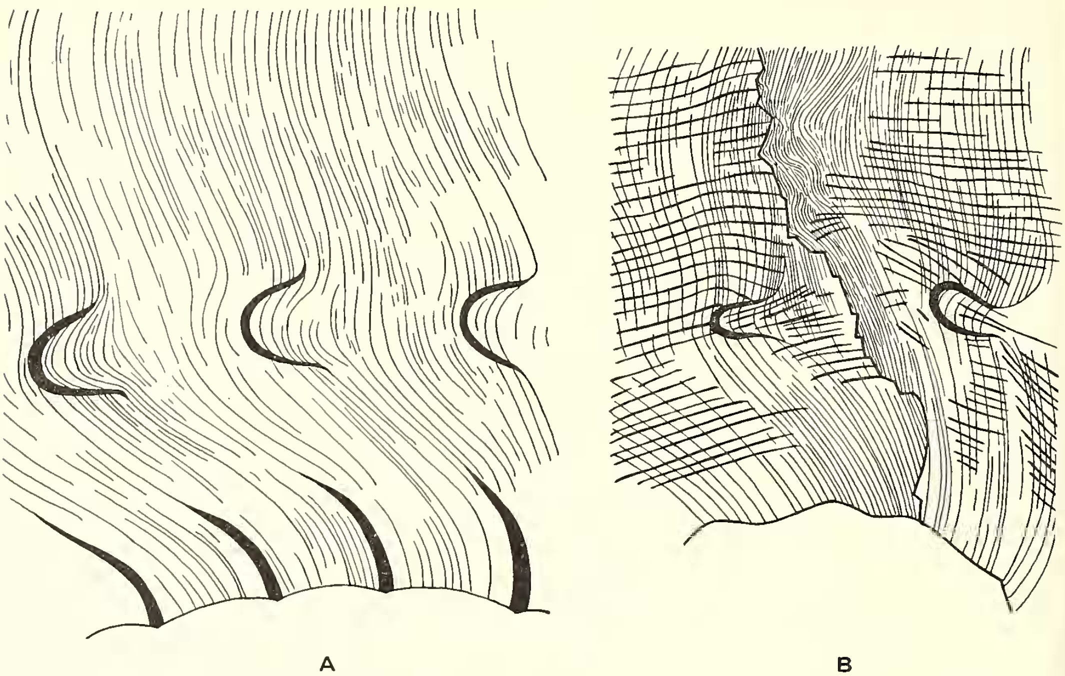
followed. After the nucleus, which is always smooth, two or three fine spiral lines appear on the upper and lower sides in the majority of the investigated individuals. After one or two whorls they disappear even if a renewed spiral ornament occurs later on the teleoconch (Pl. 107, fig. 16). In only three species is the protoconch completely smooth (Pl. 107, fig. 15). A boundary between the proto- and teleoconch can neither be traced through a particularly accentuated interruption in growth (varix), nor through a sudden onset of the adult sculpture. The number of larval whorls can therefore not be determined. When the shell is biconcave the protoconch is commonly slightly raised (text-fig. 3O), and when convexo-concave a little depressed (text-fig. 3C).

Teleoconch

Simple ribs. After one or two whorls, ribs appear more or less contemporaneously with the onset of clear growth-lines. They consist at first of weak swellings in the keel region, but with progressive growth they become enlarged as periodic ridges reaching to the suture on the upper and lower side, and running parallel with the growth-lines. On the interior of the shell this sculpture is either totally unreflected or only barely detectable, so that steinkerns of strongly ribbed forms may be perfectly smooth. As the growth-lines are not noticeably denser on the ribs themselves than between them, they are more likely to have been produced by periodically increased shell deposition than by a deceleration of growth. The number and strength of the ribs can vary considerably and is therefore of only restricted specific value.

Parabolic ribs. Long known in certain ammonites (especially perisphinctids) the significance of so-called parabolic ribs has often been discussed. In both ammonites and gastropods they are morphogenetically distinguishable from simple ribs. In form they are similar to simple ribs, but the course of the growth-lines is different. At regular intervals a growth-line (parabolic line) swings backwards in the keel region forming a parabolic notch and truncating the earlier growth-lines (text-fig. 1A). This is even more clearly seen on shells with a spiral sculpture since the sculpture itself is also cut off in the area of the parabolic notch. To some extent the spiral elements curve in sympathy with the notch and thus hint at the following discontinuity in growth (text-fig. 1B). The parabolic notch may be developed as a shell ridge (*D. albinatiensis*), or as a node (*D.* cf. *gümbeli*), or may take the form of a longitudinally open spine (*D.* (*P.*) *angusta*). In the last case the growth-lines are practically continuous.

The truncation of earlier growth-lines and the development of special sculpture features show that the normal growth of the shell was interrupted at these points. The finger-like protrusions of the mantle concomitant with the parabolic nodes or notches possessed the ability, on the one hand for resorbtion, and on the other, for shell secretion As is often the case with the siphon it may have projected beyond the calcareous envelope which it depositated. In normal shell formation the parabolic notch was first closed before new material was added to the shell margin. Only then did a marked cessation of growth occur, since: firstly, in *D.* (*P.*) *angusta* the end of a strong inner varix (former peristome) does not lie immediately beneath the parabolic notch but shortly mouthwards of it; secondly, the existing peristome was only formed after the infilling of the parabolic notch (however, in this final growth stage the last 2–3 ribs are often simple); and thirdly, a clear concentration of growth-lines owing to decelerated growth is only visible immediately after the parabolic line. In this area shell damage which affected the earlier peristome is often found (text-fig. 1B).



TEXT-FIG. 1. Parabolic nodes and course of the growth-lines from the suture to the middle of the outer side (raised parts of the shell in black). A. *Discohelix* (*D.*) cf. *albinatiensis* Dumortier, Ga 1347/14, ×13. B. *Discohelix* (*Pentagonodiscus*) *augusta* n. sp., with healed injury in a former peristome, Ga 1347/50, ×12, 5.

From this it can be concluded that the parabolic notch may not itself be equated with a former aperture, in other words, a halt in growth (of course, strictly speaking each growth-line, and therefore also the parabolic line, represents a temporary shell margin). It is rather a part of a not wholly continuous process of shell secretion between two protracted interruptions in growth, although locally the contrary, namely resorbtion, occurs. Observation of recent gastropods has shown that shell secretion between two varices occupies only a few days and that a long pause follows thereafter, in which the peristome is only strengthened by internal varices or ribs (Fretter and Graham 1962, p. 64). For this reason gastropods in which the shell margin lies within the rapid growth phase are rarely found. The same growth process explains why a parabolic line has never been observed as the final peristome in ammonites. As the extension of the mantle withdrew the parabolic notch which it had produced was infilled, a process that bearing in mind the speed of growth in gastropods could probably have been completed within a few hours. Only later was growth interrupted, which in perisphinctids is commonly indicated by deep constrictions equivalent to the inner varices of gastropods. It remains unknown whether the temporary finger-like extensions of the mantle had a physiological function in addition to the formation of parabolic notches and hollow spines. Nothing is known of this in gastropods either.

The interpretation of the parabolae of perisphinctids given by Schairer (1967, p. 26) is incorrect. He proposed as an explanation that 'the shell at certain points was more slowly deposited than at others' (author's translation). If such were the case the growth-lines would be of different density around the curve of the parabolic notch, but this is not so. Moreover, from Schairer's fig. 11, one can see that on the parabola the sculpture (in this case ribs as the author had only steinkern material) is indeed truncated. To my knowledge only Schindewolf (1934, p. 342, text-fig. 9) has demonstrated that the parabolae of ammonoids (here Upper Devonian clymenias) originated through local resorbtion.

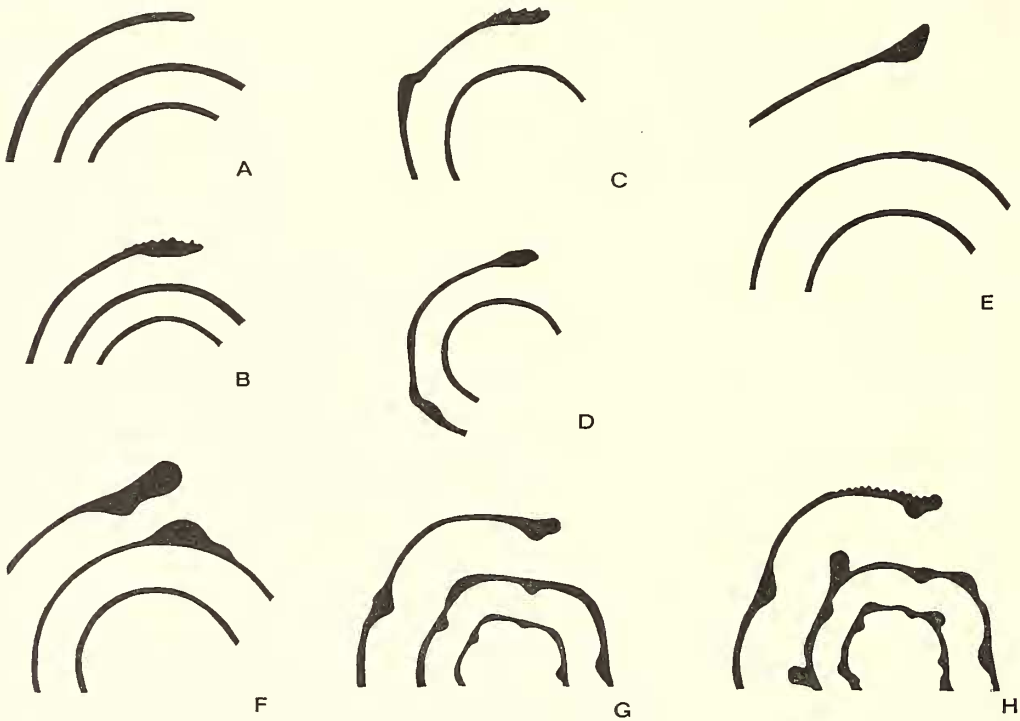
Spiral ornament. Beginning with an intermediate growth-stage, commonly on the last 2–3 whorls, fine spiral lines are formed as result of a folding of the mantle edge. They appear first in the keel region and gradually encroach onto the sides, and together with the growth-lines and ribs produce a retiform sculpture typical of many gastropods. Their number and strength may vary considerably between specimens of equal dimensions, and spiral lines are therefore of only restricted value in the differentiation of species of *Discohelix*. For example in the case of *D. albinatiensis* they can be either equally spaced over the visible part of the whorl or only developed in the keel region, and thus show a transition to specifically inseparable shells without any spiral ornament (*D*. cf. *albinatiensis*).

Peristome (text-fig. 2). Owing to the pure calcareous facies from which the whole of the material was collected, in no specimen could the peristome be completely cleared and the structures on the inside of the shell made visible. They could only be investigated in section, and the various types are best illustrated when cut in a longitudinal direction.

In the simplest case the shell margin can only be recognized through a marked concentration of the growth-lines, without any alteration of the peristome profile (e.g. *D. dictyota*, text-figs. 2A, 3E). Probably not to be specifically separated from this type is a peristome which is gradually thickened by the addition of new shell substance on the inner side, and which therefore appears somewhat narrowed in cross-section (e.g. *D. albinatiensis, D. conica, D*. cf. *crenulata*—text-figs. 2B, 3B, D, G, C). It may be preceded on the last whorl by one or two similar deposits formed during a pause in growth, but their position is random (text-figs. 2C, D).

The broadened, trumpet-like peristome is strengthened by an inner varix on the outer lip (e.g. *D. levis*, text-fig. 2E, 3L), and the aperture may also be narrowed by an inner varix on the inner lip (e.g. *D. cotswoldiae*, text-fig. 2F), The highest degree of specialization is achieved when these last two aperture types are repeated at regular intervals (*D*. (*P.*) *reussii* and *D*. (*P.*) *angusta*—text-figs. 2G, H).

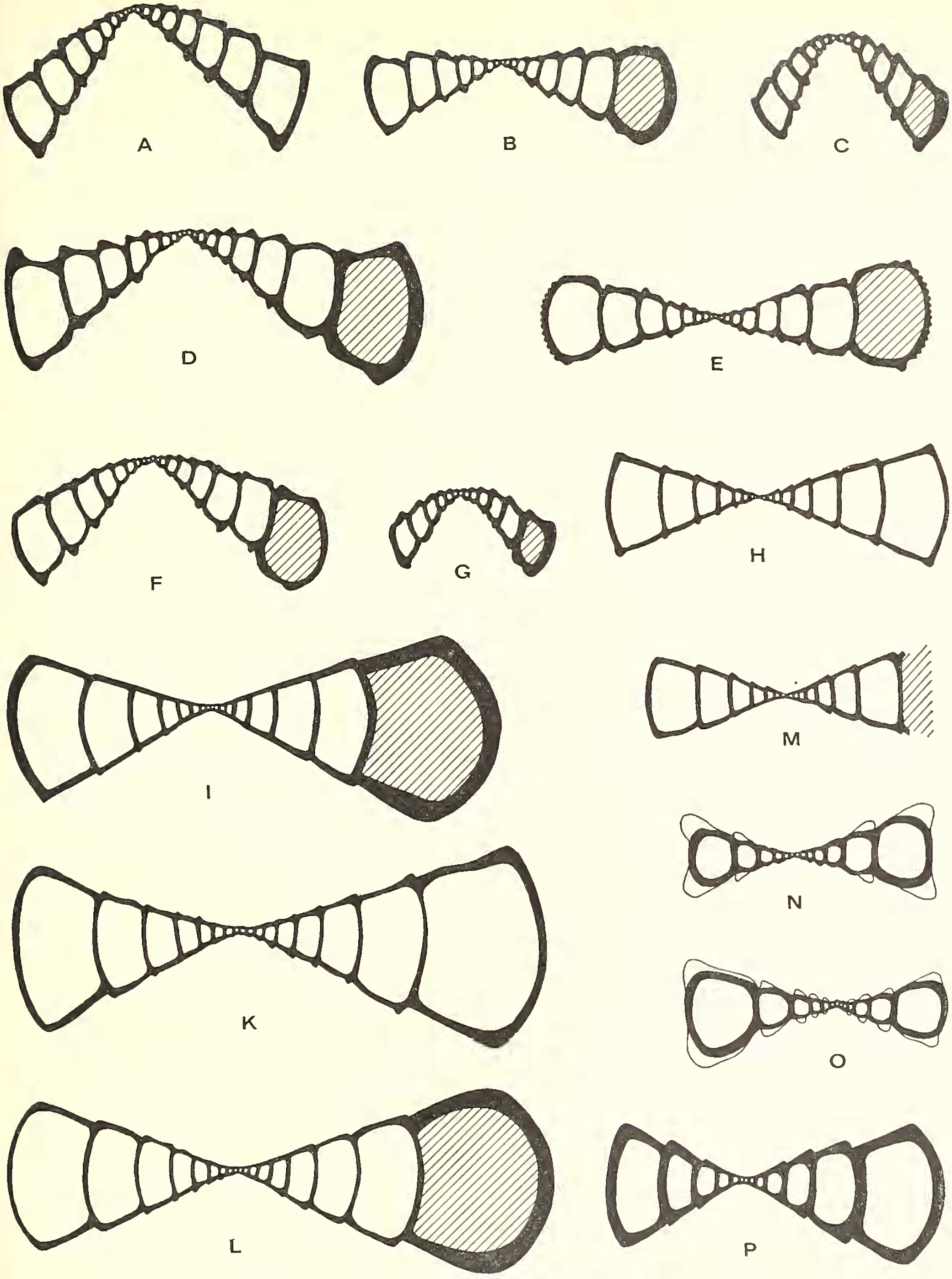
Cross-section (text-fig. 3). A cross-section passing exactly through the protoconch illustrates best the considerable variety of form within *Discohelix*. The mean spiral angle may lie between the wide boundaries of 125° to 220°, and the mean umbilical angle between 65° and 145°. The comparison of these two angles in one specimen, and the weak trochospiral coiling of the protoconch, show that perfect bilateral symmetry is not achieved in *Discohelix*. Transitions exist between a slightly concave, a plane, and a convex spire, so that this character cannot always be given specific significance. *D. albinatiensis* shows the greatest variability in this way and may occur with a plane (sometimes even slightly concave) to a clearly convex spire (text-figs. 3B, A). In one and the same individual



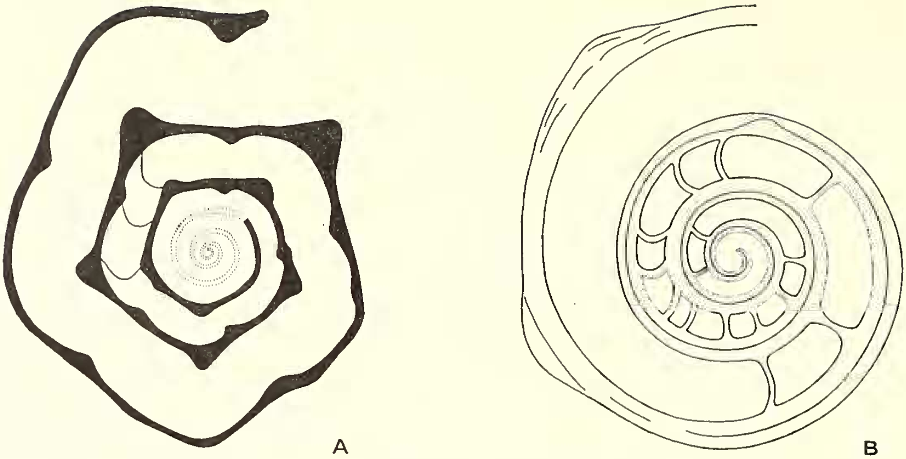
TEXT-FIG. 2. Types of peristomes (longitudinal sections), ×3, 1. A. *Discohelix* (*D.*) *dictyota* n. sp., Ga 1347/4. B. *Discohelix* (*D.*) *albinatiensis* Dumortier, Ga 1347/12. C. *Discohelix* (*D.*) *conica* n. sp., Ga 1347/28. D. *Discohelix* (*D.*) *conica* n. sp., Ga 1347/29. E. *Discohelix* (*D.*) *levis*, n. sp., Ga 1347/41. F. *Discohelix* (*D.*) *cotswoldiae* (Lycett), Ga 1347/48. G. *Discohelix* (*Pentagonodiscus*) *reussii* (Hörnes, Ga 1347/56. H. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp., Ga 1347/51.

the degree of involution may change so that the cross-section loses its axial (mirror-image) symmetry.

Septa. Septa closing off the uninhabited parts of the shell were shown by Knight (1934, p. 140) to be typical for the Euomphalidae. However, although many longitudinal sections were prepared for the species investigated here, septa were observed in only a few cases. They were found in the first 2–3 whorls but showed no regularity in either number (3–15) or distance from one another (text-fig. 4B). In one specimen of *D.* (*P.*) *angusta* three septa were found lying against the inner varices towards the end of the penultimate whorl (text-fig. 4A). This very late deposition of septa is surprising and permits no generally applicable conclusion about the length of the visceral mass.



TEXT-FIG. 3. Cross-sections, ×3, 1. A. *Discohelix* (*D.*) *albinatiensis* Dumortier, Ga 1347/9. B. *Discohelix* (*D.*) *albinatiensis* Dumortier, Ga 1347/7. C. *Discohelix* (*D.*) *conica* n. sp., Ga 1347/24. D. *Discohelix* (*D.*) cf. *albinatiensis* Dumortier, Ga 1347/15. E. *Discohelix* (*D.*) *dictyota* n. sp., Ga 1347/2. F. *Discohelix* (*D.*) cf. *crenulata* (Moore), Ga 1347/19. G. *Discohelix* (*D.*) cf. *crenulata* (Moore), Ga 1347/23. H. *Discohelix* (*D.*) cf. *calculiformis* Dunker, Ga 1347/42. I. *Discohelix* (*D.*) *centricosta* n. sp., Ga 1347/31. K. *Discohelix* (*D.*) *costata* n. sp., Ga 1347/35. L. *Discohelix* (*D.*) *levis*, n. sp. Ga 1347/37. M. *Discohelix* (*D.*) *cotswoldiae* (Lycett), Ga 1347/45. N. *Discohelix* (*D.*) cf. *gümbeli* Ammon, Ga 1347/49. O. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp., Ga 1347/52. P. *Discohelix* (*Pentagonodiscus*) *reussii* (Hörnes), Ga 1347/55.



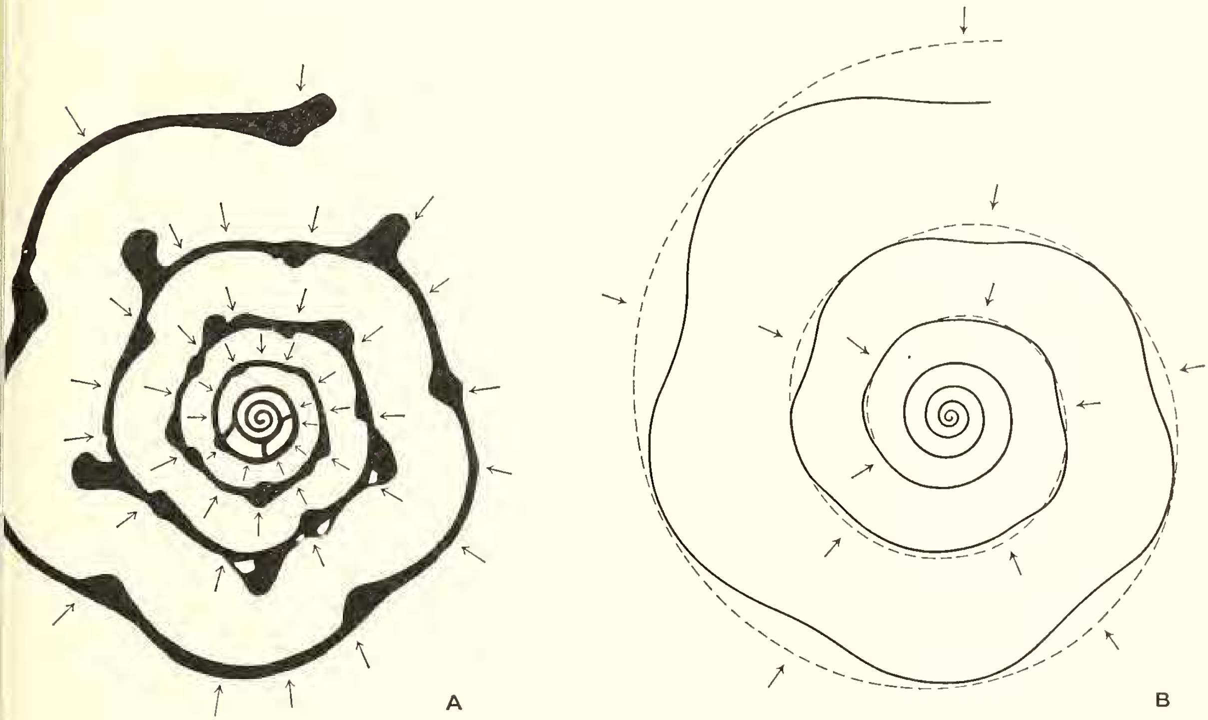
TEXT-FIG. 4. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp. A. Ga 1347/54, longitudinal section with three septa towards the end of the penultimate whorl (inner whorls not preserved), ×3·2. B. Ga 1347/51, inner whorls with septa, ×25.

GROWTH

In smooth shells no clearly marked interruptions in growth can be read from the density of the growth-lines. Therefore, the formation of the shell must have been more or less continuous. The same applies to shells with simple ribs, but those with parabolic ribs grew discontinuously, as previously discussed (p. 555). Similarly the regular inner varices following one another at intervals of 69° to 75° (mean 71·5°) in *D.* (*P.*) *reussii*, indicate periodic phases of shell deposition between long pauses (text-fig. 5).

TEXT-FIG. 5. *Discohelix* (*Pentagonodiscus*) *reussii* (Hörnes), Ga 1347/56, longitudinal section, ×6·3.

These two growth-rhythms, expressed in the one case by parabolic ribs and in the other by inner varices, occur together and interfere with one another in *D.* (*P.*) *angusta*. As in *D.* (*P.*) *reussii* the inner varices exhibit pentagonal symmetry (means of 70·4°, 70·7°, and 76° in three measured specimens), and between them three (on inner whorls sometimes two) parabolic ribs are intercalated. These ribs tend to arrange themselves in groups of three towards the last whorl. In this way the first formed parabolic rib of such a group coincides with an inner varix (text-figs. 6A, 7). (The outer varices, seen externally, cannot be exactly transferred into the longitudinal section; their position may therefore be slightly different.)

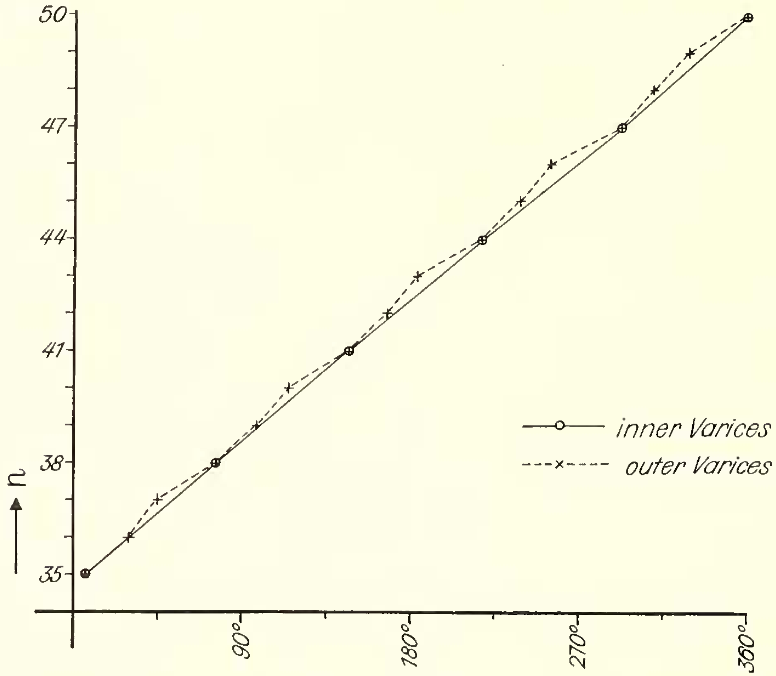


TEXT-FIG. 6. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp. A. Ga 1347/53, longitudinal section, ×6·3 (arrows indicate outer varices). B. Ga 1347/51, extrapolation of the normal logarithmic spiral (hatched line) from the regularly coiled inner whorls in comparison to the actual spiral (unbroken line), ×6.

Thus if one considers the parabolic features as brief discontinuities and the inner varices as drawn out breaks in shell secretion, then *D.* (*P.*) *angusta* shows complicated double-phased growth, the control of which is unknown.

The subgenus *Pentagonodiscus* assumes a pentagonal outline in the last 2–2½ whorls. In text-fig. 6B the normal logarithmic spiral of the regularly coiled inner whorls has been extrapolated omitting the various irregularities of the shell (inner varices, ribs). This clearly shows that the aberrant shell form commences with the first inner varix and becomes more accentuated as the varices increase in strength towards the aperture. The most prominent deviations from a logarithmic spiral occur at the points of periodic constrictions of the former peristomes. In the intervening growth-phases the spiral is again followed and thus shows itself to maintain control of the pentagonal coiling.

Among the gastropods, there appear to be only two cases of angular instead of regular spiral coiling: *Triangularia paradoxa* Frech and *Tremanotus polygonus* Barrande. The first has a triangular, and the latter a pentagonal outline. Nothing is known of the internal structure of either of these two species. Periodically constricted apertures were probably also formed and might be revealed by inner varices.



TEXT-FIG. 7. *Discohelix* (*Pentagonodiscus*) *angusta* n. sp. Ga 1347/53. Diagrammatic view of the intervals of the inner and outer varices on the last whorl (n = no. of outer varices, counted from the centre).

Deviations from a logarithmic spiral are widely distributed among ammonoids, but commonly affect only the last body chamber. Triangular coiling in early ontogenetic stages, producing an extremely aberrant shell form, is found solely in a few clymenids (*Soliclymenia*, *Wocklumeria*, *Parawocklumeria*) and goniatites (*Paralegoceras*) (see Schindewolf 1937, p. 110 et seq.). It is conceivable that periodic narrowing of the aperture was also responsible. Deep constrictions, signifying a former aperture at the points of strongest deviation from the normal spiral, occur in two of these genera (*Wocklumeria*, *Parawocklumeria*) and support this supposition. A narrowed body chamber in early ontogenetic stages, remaining unresorbed, and periodicity in growth lead automatically to an angular instead of a spiral shell form. If one imagines further shell growth after the last known peristome of e.g. *Oecoptychius refractus* (Reinecke), an angular outline must necessarily be the result. Not to be confused with such genuine angular forms are those in which the umbilicus has a polygonal outline as a result of deep constrictions (e.g. *Morphoceras*, some perisphinctids). In longitudinal section they have a perfectly regular logarithmic spiral.

No attempt has been made here to fully explain the phenomenon of triangular ammonoids. The control of such aberrant growth remains as speculative as in polygonally coiled gastropods.

MODE OF LIFE

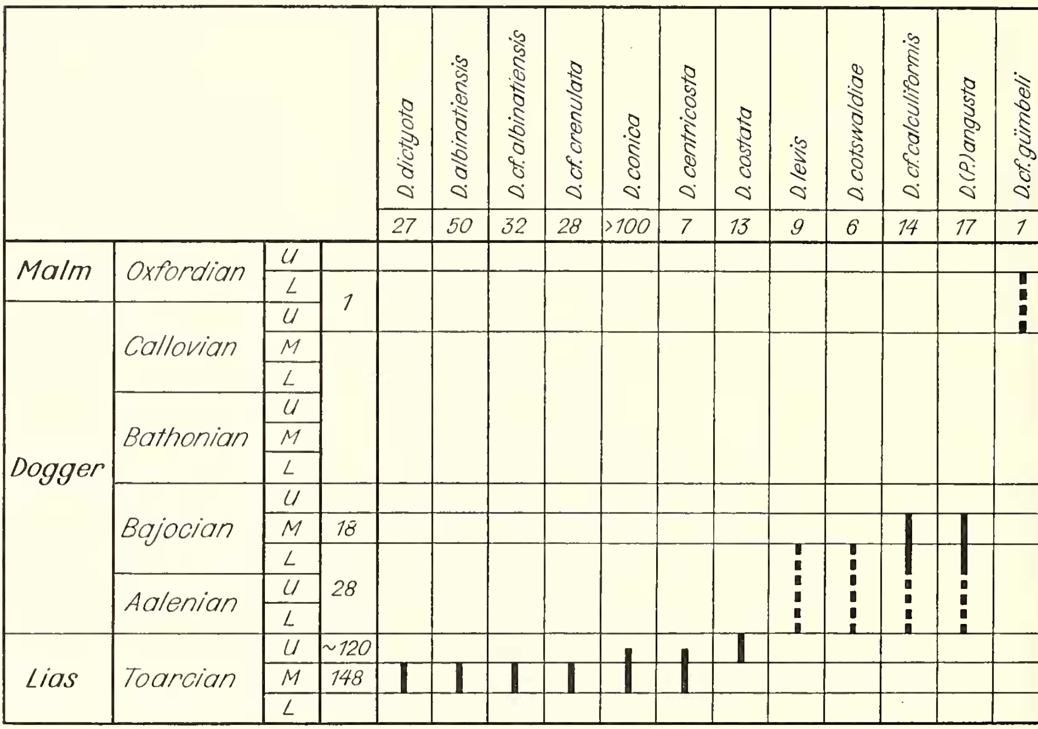
The planispiral coiling of many *Discohelix* species is reminiscent of ammonoids and suggests adaption to a nektonic mode of life. Thus Koken (1897, p. 42) proposed that the Upper Triassic *Kokenella* (Pleurotomariacea), which is first coiled in a trochospiral and later in a planispiral, was adapted to a free swimming in deep sea. However, no recent gastropod with an almost symmetrical shell is known to be capable of active swimming. A single exception are the pelagic Heteropoda (e.g. *Atlanta*) with a weakly calcified, very thin or wholly vestigial shell. They cannot be compared with the thick-shelled, often strongly sculptured *Discohelix*, for which only a benthonic mode of life can be considered. If the planispiral coiling were an adaption to a nektonic mode of life, then this feature would normally tend to be realized as a result of selection. It turns out, however, to be extremely variable, not only on the specific but also on the generic level.

The disc shape, in fact, would appear to be a disadvantage since it is much more susceptible to water movement than a helicocone. This can scarcely have been compensated for by the narrow whorls and the small aperture, indicating a correspondingly small and weak foot. For this reason the most favourable environment for *Discohelix* may have been in quiet sublittoral water or in the shelter of reefs rather than in a disturbed littoral. In a vertical position the pentagonal form can be seen to have an advantage over the spiral form, since the angularity provides a kind of resting surface (cf. *Murex*) allowing the animal a greater stability on the sea-floor. The efficiency of this is increased through the support of lateral spines in *D.* (*P.*) *angusta*.

DEVELOPMENT AND VALUE AS INDEX FOSSILS

There are still great gaps in our knowledge of the development of the Euomphalidae in the Triassic. For this reason the exact origin of the genus *Discohelix* has not yet been elucidated. Several Triassic forms described as *Euomphalus* belong to *Woehrmannia*, but the majority are insufficiently known for an exact generic determination.

Typical biconcave shells with more or less bilaterally symmetrical whorls and upper and lower keel appear for the first time in the lowermost Liassic. A greater variety of forms are known from the Sinemurian, especially from the Northern Calcareous Alps (Hierlatz-facies), amongst which are some with a plano-concave cross-section. The transition from biconcave to convexo–concave shells probably occurred several times independently, as has been observed in *D. albinatiensis* (p. 558). A special off-shoot of pentagonally coiled forms (subgenus *Pentagonodiscus*) also commenced in the Sinemurian but with only two stratigraphically isolated species, it has not yet been fully verified. The observed variation of individual features reduces their phylogenetic value and makes it necessary to separate species according to character combinations. Despite the approximately forty known (many insufficiently) *Discohelix* species their lines of evolution can only be traced at a few points. Their stratigraphical distribution has not been proved because of their sparsity, occurrence as fissure-faunas, and the failure of accompanying index fossils. Therefore the well dated material presented here assumes a special stratigraphical value. From text-fig. 8 it can be seen that the species have only a very short range, extending through only one or a few zones. Similar conclusions can be drawn from the stratigraphical information given by Hudleston (1892, pp. 315–21) for the English Middle Jurassic.



TEXT-FIG. 8. The stratigraphical distribution of *Discohelix* in the condensed Jurassic of Rocca Busambra (Western Sicily); numbers indicate number of specimens.

The strong condensation in the sections made it necessary to use substages instead of zones for the time-scale in text-fig. 8. In three cases the boundaries of the substages could not be drawn since up to five zones are inseparably concentrated in one stratigraphical unit (Wendt 1965, p. 300). For this reason the exact range of some of the species cannot be given. The representatives of *Discohelix* which begin the fossil record in the Middle Toarcian (Bifrons Zone) may have originated earlier. The absence of species from the base of the Bathonian to the Upper Callovian is owing to a stratigraphic gap characteristic of the west Sicilian Jurassic. A diminution of the *Discohelix* fauna is already evident earlier, and the last representative on the Dogger–Malm boundary is almost coincident with the extinction of the genus in the Lower Oxfordian.

It should not be overlooked that the stratigraphical range of the species investigated here is based on a series of sections from a single locality. To date it has been verified in two cases by specimens from the Northern Calcareous Alps. Furthermore well-dated material of *Discohelix* is wanted to complete and, if necessary, correct the ranges of the various species.

SYSTEMATIC DESCRIPTIONS

Only two imperfectly preserved examples were available to Dunker when he established the genus *Discohelix* in 1847, so that even he himself was uncertain of its individuality five years later (see footnote in Reuss 1852, p. 116). Rich material allowed Stoliczka (1861, p. 180 et seq.) to distinguish *Discohelix* from *Euomphalus* and to define it precisely for the first time. Without altering this concept of the genus Cossmann (1915, p. 133 et seq.) included in it both Triassic and Cretaceous species, although they did not completely pass within his diagnosis. In the same publication he proposed the genus *Colpomphalus* (1915, p. 136) for forms with a convex spire transitional to *Discohelix*. This gradation is in fact so continuous, even in one and the same species (see p. 558), that *Colpomphalus* can no longer be maintained as an independent unit. Among the Triassic predecessors of *Discohelix*, *Amphitomaria* Koken differs through its prosocyrt growth-lines on the outer side, and *Anisostoma* Koken through its peculiar, deflected peristome. (Specimens placed in the latter genus, from which the aperture has been broken, could, in fact, be early members of *Discohelix*.)

Genus DISCOHELIX Dunker 1847

Type species. D. calculiformis Dunker 1847.

Diagnosis. Widely to extremely widely umbilicate representatives of the Euomphalidae, with numerous, not overlapping whorls of trapezoidal cross-section, with an upper and lower keel. Mostly dextral, rarely sinistral. Spire concave, plane or convex. Protoconch homeostrophic, not sharply separated from the teleoconch. Growth-lines on the upper and lower sides prosocline, on the outer side opistocyrt. Ornament collabral and/or spiral. Peristome more or less tangential to foregoing whorl, its outline parallel to the axis of coiling, simple or with thickened outer and/or inner lip. Operculum unknown.

Distribution. Triassic? Jurassic (Hettangian to Oxfordian).

Synonym. Colpomphalus Cossmann 1915.

Discohelix (*Discohelix*) *dictyota* n. sp.

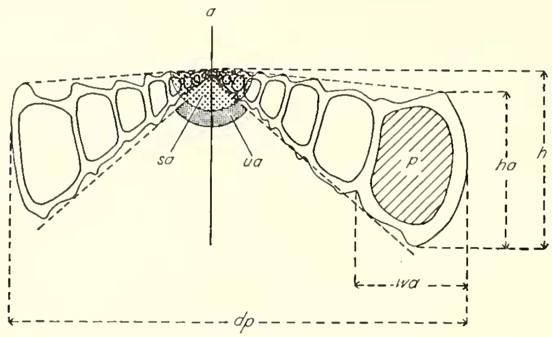
Plate 107, figs. 1–8; text-figs. 2A, 3E

Derivation of name. dictyotus = retiform.

Holotype. Ga 1347/1. Plate 107, figs. 1–4.

No.	*dp*	*d*	*h/d*	*ha/wa*	*nw*	*nt*	*sa*	*ua*
Ga 1347/1		20·0	0·29	1·49	9	34		
Ga 1347/2	18·3		0·28	1·33	8	(30)	214°	145°
Ga 1347/3		16·4	0·29	1·78	8	33		

Diagnosis. Dextral, spire concave; protoconch spirally ornamented, teleoconch with retiform sculpture; peristome unthickened.



TEXT-FIG. 9. Shell measurements. a = axis of coiling, dp = maximum diameter measured at peristome (in mm.), h = height of shell, ha = height of aperture, p = cross-section through peristome (hatched), sa = mean spiral angle, ua = mean umbilical angle, wa = width of aperture.

Additional abbreviations in the measurement-tables: d = diameter (in mm.), nt = number of tubercles (nodes), numbers in ( ) referring to half whorls, nw = number of whorls.

Description. Fine ribs appear after the protoconch contemporaneously with the onset of clear growth-lines. They develop on the keel as nodes, and with good preservation may be recognized on the last whorls as a parabolic feature. On this last whorl the spiral lines, 7–10 on the upper and lower sides and 16–20 on the outer side, are strongest; they fail on the inner whorls of the teleoconch. The final peristome shows no special structure. Before it, on two specimens, a short pause in growth is indicated by a gentle angulation in the shell outline.

Discussion. D. reticulata Stoliczka shows a similar sculpture, the spiral lines being restricted to the outer side, however, the whorls are more compressed, and broader than high in cross-section. *D. orbis* (Reuss) can be distinguished by its much finer ornament and clearly differentiated keel, and *D. dunkeri* Moore by its fewer nodes and plano-concave cross-section.

Distribution. Middle Toarcian (Bifrons Zone).

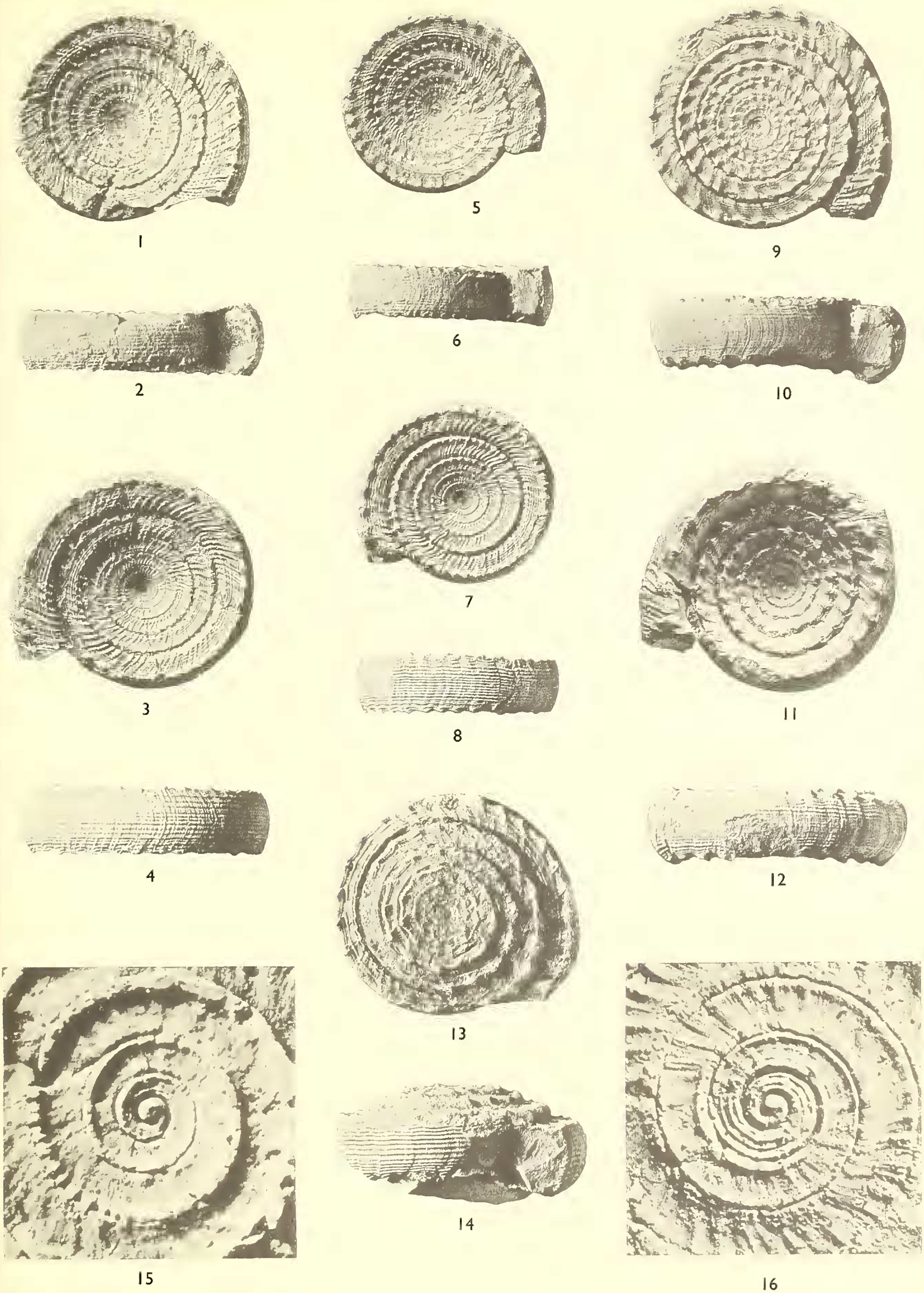
Discohelix (*Discohelix*) *albinatiensis* Dumortier 1874

Plate 107, figs. 9–15; Plate 108, figs. 8–10; text-figs. 2B, 3A–B

1874 *Discohelix Albinatiensis* Dumortier, p. 284, pl. 59. figs. 3–5.
?1892 *Straparollus pulchrior* Hudleston, p. 318, pl. 25, fig. 9.

EXPLANATION OF PLATE 107

Figs. 1–4. *Discohelix* (*D.*) *dictyota* n. sp., holotype. Ga 1347/1, ×2.
Figs. 5–8. *Discohelix* (*D.*) *dictyota* n. sp., Ga 1347/3, ×2.
Figs. 9–12. *Discohelix* (*D.*) *albinatiensis* Dumortier, Ga 1347/6, ×3.
Figs. 13–14. *Discohelix* (*D.*) *albinatiensis* Dumortier, Ga 1347/8, ×3.
Fig. 15. *Discohelix* (*D.*) *albinatiensis* Dumortier, Ga 1347/11. Inner whorls with protoconch, ×20.
Fig. 16. *Discohelix* (*D.*) cf. *albinatiensis* Dumortier, Ga 1347/14. Inner whorls with protoconch, ×20.



WENDT, *Discohelix* from the Tethyan Jurassic

Lectotype (here selected). Dumortier 1874, pl. 59, figs. 4–5.

No.	*dp*	*d*	*h/d*	*ha/wa*	*nw*	*nt*	*sa*	*na*
Ga 1347/5	15·3		0·29	1·55	8	(16)	184°	120°
Ga 1347/6	14·2		0·32	1·43	8	27		
Ga 1347/7	14·2		0·30	1·48	8	(13)	188°	117°
Ga 1347/8		13·2	0·42	1·22	8	25		
Ga 1347/9		14·4	0·48	1·47	9	(18)	132°	81°
Ga 1347/10		12·4	0·33	1·63	8	12		

Diagnosis. Dextral, spire weakly concave, plane, or weakly convex; protoconch smooth, retiform sculpture on teleoconch; peristome thickened.

Description. The majority of the available specimens are plano-concave, several specimens, however, have a slightly concave or a more or less strongly convex spire. The larval whorls are free of sculpture, with an angulation near the suture, slightly concave upper side, and a smooth keel. The ornament of the teleoconch, beginning after $1\frac{1}{2}$–2 whorls, is similar to, but somewhat coarser than in *D. dictyota*. 20–27 parabolic nodes may be counted on the keel. 10–20% fewer nodes are present on the lower keel, thus emphasizing the asymmetry of the shell. Seven examples varying in diameter between 7 and 13 mm. stand apart from the remainder of the material in that the nodes are more widely spaced (12–15 instead of 20–23 on typical individuals, see Pl. 108, figs. 8–10). A clear spiral ornament begins only after a diameter of 10 mm. has been reached. It may completely fail on the upper and lower sides and be restricted to a small area adjacent to the keel on the outer side. The peristome is internally thickened and therefore narrowed.

Discussion. The larval whorls and peristome were not preserved in the material used by the authors cited in the synonymy, so that the present specimens can only be named with some reservation. Those with the most raised spire cannot be distinguished in cross-section and sculpture of the teleoconch from *D. exsertus* (Hudleston 1892, p. 320, pl. 26, figs. 3–4).

Distribution. Middle Toarcian (Bifrons Zone). The type was thought by Dumortier to have come from the Opalinum Zone, but was found in a loose block of uncertain stratigraphic origin. According to Hudleston (1892, p. 319) *D. pulchrior* occurs rarely in the Murchisonae Zone.

Discohelix (*Discohelix*) cf. *albinatiensis* Dumortier 1874

Plate 107, fig. 16; Plate 108, figs. 1–7; text-figs. 1A, 3D

? 1935 *Discohelix albinatiensis* Dumortier; Roman, p. 32, pl. 6, figs. 1, 1*a*.

No.	*dp*	*d*	*h/d*	*ha/wa*	*nw*	*nt*	*sa*	*na*
Ga 1347/13	22·9		0·37	1·40	9	29		
Ga 1347/14		21·0	0·41	1·96	9	30		
Ga 1347/15	19·4		0·39	1·52	9	(16)	171°	99°
Ga 1347/16		16·3	0·47	1·73	8	(14)	165°	90°

Description. In contrast to typical members of the species spiral sculpture is totally lacking on the last whorls, but 2–3 spiral lines may be traced on the upper side of the protoconch. From these two characters a decisive separation from *D. albinatiensis* is not possible.

Distribution. Middle Toarcian (Bifrons Zone).

Discohelix (*Discohelix*) cf. *crenulata* (Moore 1867)

Plate 108, figs. 11–16; text-figs. 3F, G

cf. 1867 *Solarium crenulatum* Moore, p. 90, pl. 4, figs. 19–20.

No.	*dp*	*d*	*h/d*	*ha/wa*	*nw*	*nt*	*sa*	*ua*
Ga 1347/19	14·4		0·46	1·41	9	(30)	148°	87°
Ga 1347/20		13·3	0·38	1·42	8	50		
Ga 1347/21		12·8	0·52	1·50		54		
Ga 1347/23	7·7		0·57	1·36	7		147°	76°

Description. The shell form of this dextrally coiled species varies from almost plano-concave (*sa* = *c.* 170°) to clearly convexo-concave. The mean umbilical angle varies correspondingly between relatively wide boundaries. The protoconch has distinct spiral lines, and after $1\frac{1}{2}$–2 whorls fine ribs appear which rise to small nodes on the keel. Later, spiral lines reappear so that the sculpture is similar to that of *D. dictyota* and *D. dundriensis* (Tawney), as Hudleston (1892, pl. 26, fig. 2) figured in detail. However, the external spiral lines are seldom regularly distributed over the whole outer side of the last whorl, and a smooth band is left free in the centre.

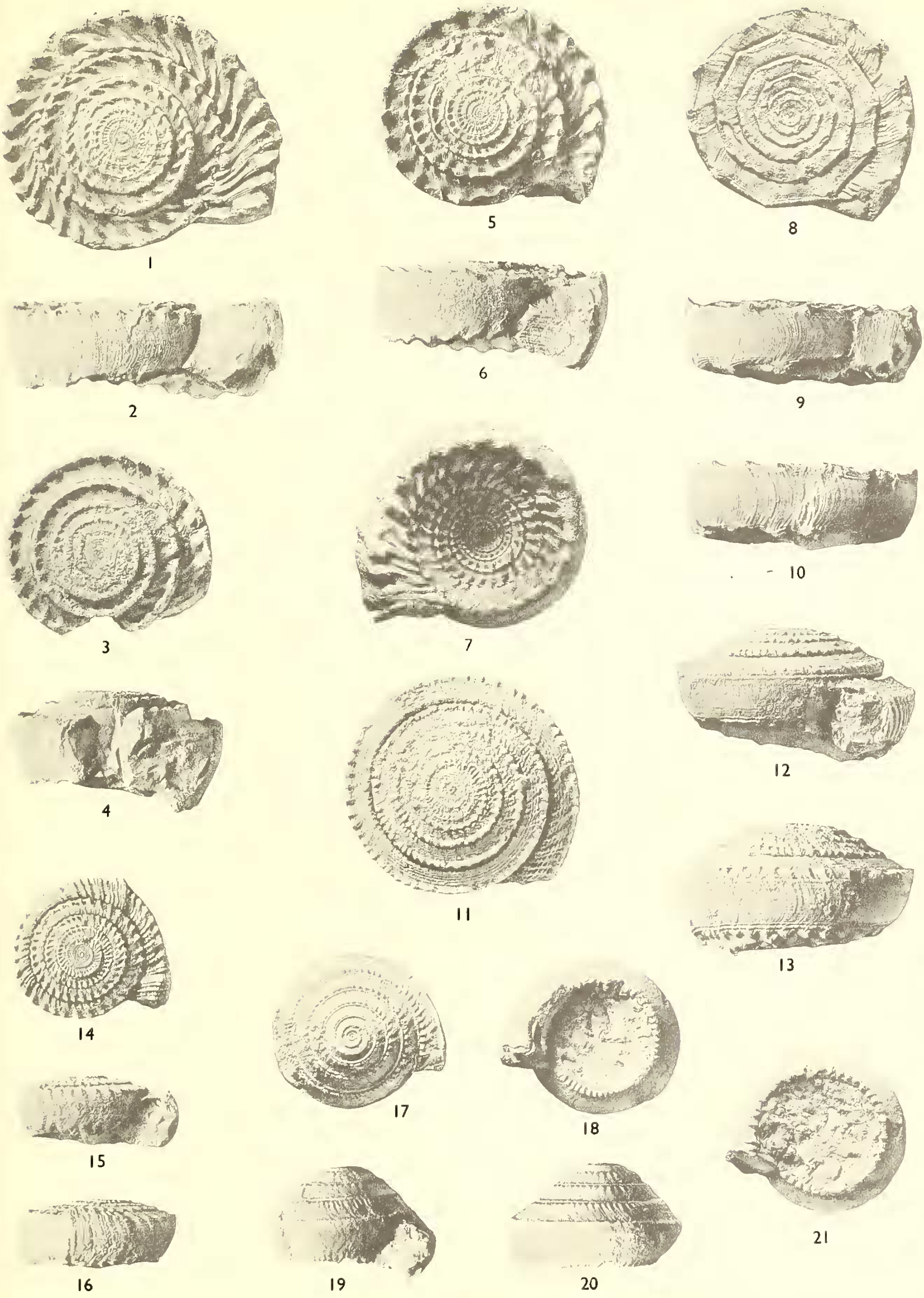
In the available material two varieties differing in their whorl number can be distinguished: one having 7 whorls at a maximum of approximately 8 mm. in diameter, and the other 8–9 whorls at 13–15 mm. in diameter. The aperture of the small examples is thickened (text-fig. 3G) and that one of the large ones is simple and unthickened (text-fig. 3F).

Discussion. Moore's figure and description do not give a clear impression of this species and it has not since been mentioned. Therefore no comparison of the shell cross-sections can be made, but aside from this the present specimens have a much wider umbilicus. A similar umbilicus is possessed by *D. crussoliensis* Roman (1935, p. 102, pl. 3, figs. 5, 5*a*), but this species is considerably more conical. *D. helenae* (Dumortier 1874, p. 141, pl. 36, figs. 1–4) has a comparable shell shape but the nodes on the keels are coarser and more widely spaced (18 in contrast to 50–60 in *D.* cf. *crenulata*).

Distribution. Middle Toarcian (Bifrons Zone). The type was said to be from the upper Middle Liassic.

EXPLANATION OF PLATE 108

Figs. 1–2. *Discohelix* (*D.*) cf. *albinatiensis* Dumortier, Ga 1347/13, ×2.
Figs. 3–4. *Discohelix* (*D.*) cf. *albinatiensis* Dumortier, Ga 1347/18, ×2.
Figs. 5–7. *Discohelix* (*D.*) cf. *albinatiensis* Dumortier, Ga 1347/17, ×2.
Figs. 8–10. *Discohelix* (*D.*) *albinatiensis* Dumortier, Ga 1347/10, ×3.
Figs. 11–13. *Discohelix* (*D.*) cf. *crenulata* (Moore), Ga 1347/21, ×3.
Figs. 14–16. *Discohelix* (*D.*) cf. *crenulata* (Moore), Ga 1347/22, ×3.
Figs. 17–21. *Discohelix* (*D.*) *conica* n. sp., holotype, Ga 1347/25, ×3.
Fig. 21. *Discohelix* (*D.*) *conica* n. sp., Ga 1347/27, ×3.



WENDT, *Discohelix* from the Tethyan Jurassic

Discohelix (*Discohelix*) *conica* n. sp.

Plate 108, figs. 17–21; text-figs. 2C–D, 3C

Holotype. Ga 1347/25. Plate 108, figs. 17–20.

No.	*dp*	*h/d*	*ha/wa*	*nw*	*sa*	*ua*
Ga 1347/24	9·1	0·64	1·52	7	124°	63°
Ga 1347/25	9·3	0·65	1·42	7		
Ga 1347/26	10·7	0·53	1·31	7½	132°	74°

Diagnosis. Small, dextral, spire convex; protoconch spirally ornamented, on teleoconch only growth-lines, smooth upper and finely tuberculated lower keel; peristome thickened.

Description. Three spiral lines can be traced on the depressed protoconch and disappear after 1–1½ whorls. From approximately the fourth whorl fine nodes appear close to the suture, stretched out in the direction of the growth-lines but not reaching the smooth upper keel. The lower keel is formed by a succession of fine tubercles which are accompanied on the outer side by 2–3 undulating spiral lines. The externally thickened peristome can sometimes be seen to have been preceded on the last whorl by 1–2 growth interruptions (text-figs. 2C–D).

Discussion. *D. conica* contrasts with the above species in having a higher spire. Furthermore the failure of spiral ornament and the smooth upper keel are good specific characters.

Distribution. Middle to lower Upper Toarcian (Bifrons to c. Thouarsense Zone).

Discohelix (*Discohelix*) *centricostata* n. sp.

Plate 109, figs. 1–7; text-fig. 3I

Holotype. Ga 1347/30. Plate 109, figs. 1–3.

No.	*dp*	*d*	*h/d*	*ha/wa*	*nw*	*sa*	*ua*
Ga 1347/30		23·0	0·31	1·51	8		
Ga 1347/31	25·6		0·35	1·29	9	217°	136°
Ga 1347/32	18·4		0·32	1·75	8		

Diagnosis. Dextral, spire concave; protoconch spirally ornamented, nepionic whorls ribbed, neanic whorls smooth; peristome trumpet-like.

Description. The shell consists of 7–9 whorls and the spire is almost as depressed as the umbilicus resulting in a nearly symmetrical cross-section. The 2–4 whorls following the spirally ornamented protoconch have weak ribs and finely tuberculate keels. These elements become less accentuated with growth. The last whorls are completely smooth or show only traces of a slight undulation. The aperture, which is only preserved in two cases, is broadened and thickened to an almost circular cross-section in the larger specimen (text-fig. 3I), and in the smaller (Ga 1347/32) is similar in cross-section to the preceding whorls.

Discussion. Without knowledge of the protoconch this species cannot be separated from *D. calculiformis* Dunker.

Distribution. Middle to lower Upper Toarcian (Bifrons to c. Thouarsense Zone).

Discohelix (*Discohelix*) *costata* n. sp.

Plate 109, figs. 12–18; text-fig. 3K

Holotype. Ga 1347/34. Pl. 3, figs. 15–18.

No.	*dp*	*d*	*h/d*	*ha/wa*	*nw*	*nt*	*sa*	*ua*
Ga 1347/34		24·8	0·42	1·83	9	29		
Ga 1347/35	25·0		0·38	1·46	8	(13)	213°	129°
Ga 1347/36	19·8		0·32	1·42	8	27		

Diagnosis. Dextral, spire concave; protoconch spirally ornamented, teleoconch ribbed; peristome thickened, somewhat broadened.

Description. 4–5 spiral lines are present on the upper and lower side of the protoconch, but are quite absent from the following whorls. They are ornamented by regular ribs which may be traceable in the nepionic stage or only on the last whorl. The outer side, between the strongly corrugated keels, is completely smooth except for fine growth-lines.

Discussion. The biconcave shell form, the failure of spiral lines, and the strong sculpture make *D. costata* a very distinctive species. A phylogenetic connection with *D. centricosta* seems probable, *D. costata* having originated from this species through a persistence of the ribbing to the last whorl.

Distribution. Upper Toarcian (c. Variabilis to Levesquei Zone).

Discohelix (*Discohelix*) *levis* n. sp.

Plate 109, figs. 8–11; text-figs. 2E, 3L

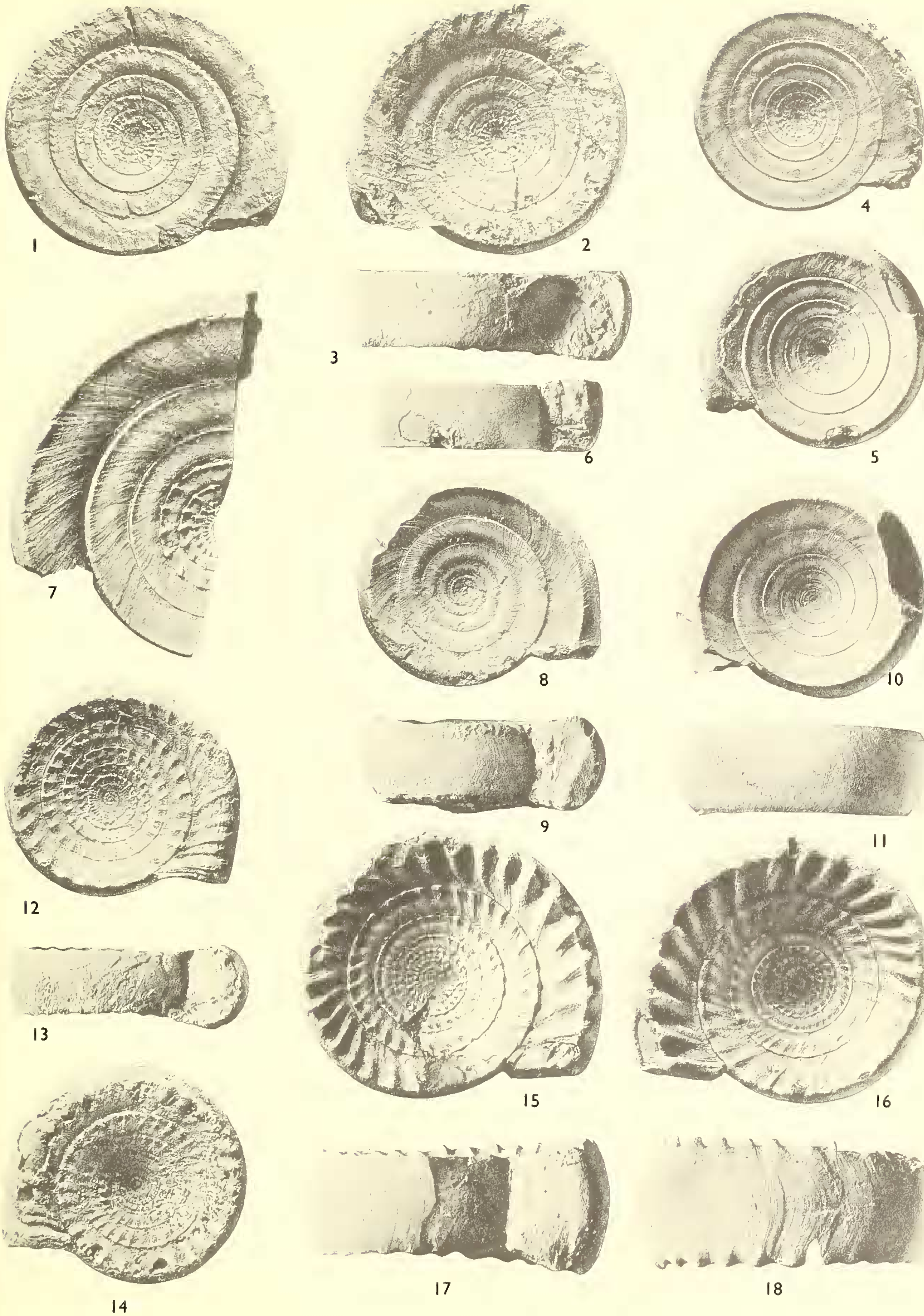
Derivation of name. levis = smooth.

Holotype. Ga 1347/38. Plate 109, figs. 8–9.

No.	*dp*	*d*	*h/d*	*ha/wa*	*nw*	*sa*	*ua*
Ga 1347/37	22·7		0·38	1·29	8	211°	124°
Ga 1347/38	19·7		0·36	1·51	8		
Ga 1347/39	15·6		0·33	1·30			
Ga 1347/40		19·8	0·37	1·59	8		

EXPLANATION OF PLATE 109

Figs. 1–3. *Discohelix* (*D.*) *centricosta* n. sp., holotype, Ga 1347/30, ×2.
Figs. 4–6. *Discohelix* (*D.*) *centricosta* n. sp., Ga 1347/32, ×2.
Fig. 7. *Discohelix* (*D.*) *centricosta*, n. sp., Ga 1347/33, ×3.
Figs. 8–9. *Discohelix* (*D.*) *levis* n. sp., holotype, Ga 1347/38, ×2.
Figs. 10–11. *Discohelix* (*D.*) *levis* n. sp., Ga 1347/40, ×2.
Figs. 12–14. *Discohelix* (*D.*) *costata* n. sp., Ga 1347/36, ×2.
Figs. 15–18. *Discohelix* (*D.*) *costata* n. sp., holotype, Ga 1347/34, ×2.



WENDT, *Discohelix* from the Tethyan Jurassic